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Ecological Stability: An Ecosystem Perspective

Classical and Current Thoughts

A Review of Selected Literature

Peter Van Voris

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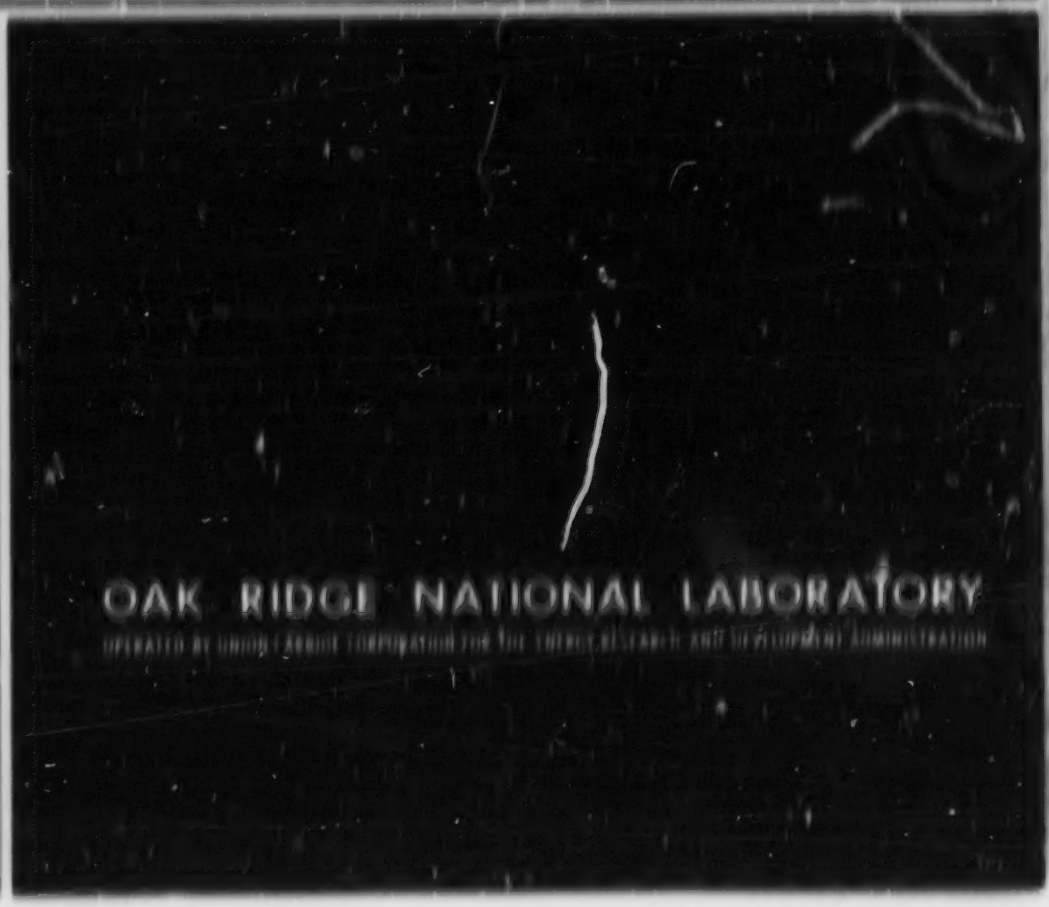

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A Review of Selected Literature

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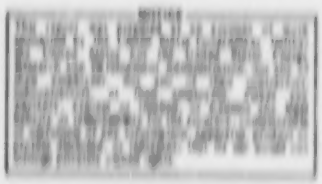

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ABSTRACT

VAN VORIS, PETER. 1976. Ecological Stability: An Ecosystem Perspective Classical and Current Thoughts. ORNL/TM-5517. Oak Ridge National Laboratory, Oak Ridge, Tennessee. 34 pp.

The term "stability", in its ecological context, has been applied to populations, communities, and, most recently, to ecosystems with such an array of meanings that it has almost become a panchreston. This review of selected literature points out the problems inherent in relying on either static measures (e.g., species diversity, connectivity, or energy balance) as a measure of complexity to arbitrarily rank the relative stabilities of ecosystems, or the dynamic approach of analysing the mathematical stability of linear or nonlinear models. The research direction emphasized is that of development of new measures of ecosystem complexity based on ecosystem level characteristics (e.g., nutrient retention, or ecosystem metabolism) and relating these measures of complexity to an a priori defined ecosystem stability.

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FOREWORD

This literature survey reviews the state-of-the-art of ecological stability theory and the available measurement technique as a first step toward the formation of new measurement concepts for ecosystem properties and stability. (The research proposal for the doctorate degree will be a separate document, but will be based on theoretical constructs developed from this document and from discussions with R. V. O'Neill, H. H. Shugart, B. S. Ausmus, and others at Oak Ridge National Laboratory).

A review of stability literature is difficult for numerous reasons. The concept has ranged from intuitive understanding, through theory, experiments, and, most recently, mathematical treatment. In synthesizing this diffuse literature, the author has discovered numerous cul-de-sacs which were purposefully explored to show where the research led and why it seemed fruitless to continue along those paths.

The term "stability" has been used in this report as it was used in each of the articles referenced to show that the authors cited had not qualified the use of the term, and to demonstrate the ambiguities surrounding the term that have been perpetuated in the literature.

INTRODUCTION AND HISTORICAL PERSPECTIVE

The great technological advances of the last century have given rise to a growing concern about man's impact on his environment. Possibly the most fundamental problem concerns ecosystem stability. To what extent may impacts to an ecosystem be absorbed before disrupting essential homeostatic mechanisms? Which ecosystems are most susceptible to disruption? What measurements of the ecosystem will predict disruption? The intent here is to review the relevant literature and attempt to synthesize patterns surrounding the concepts that have developed.

Recent publications (Botkin and Sobel 1975, Lewontin 1969, Orians 1974, Innis 1975) point out the ambiguity of the word, "stability". Orians (1975) notes that seven differing definitions have surfaced emphasizing constancy, persistence, inertia, elasticity, amplitude, cyclical stability, and trajectory stability. Other terms used to describe ecological stability include resilience, sensitivity, fragility, neighborhood stability, global stability, and frequency boundedness. These descriptors have tended to add vagueness to the concept. Thus, many semantic difficulties have arisen from careless adoption of the language of other sciences (Goodwin 1970).

There seems to have been an intuitive understanding of stability from the inception of ecology. Anton Kerner in 1863 described nature's constancy in his writings on the plant life of the Danube basin (Conard 1951). Marsh (1885) refers to the "stability of nature" when discussing the impact of the Roman Empire on the landscape of conquered provinces. An interest in, and a grasp of, ecosystem stability is clearly evidenced by these early writers.

The meaning of stability took on a new dimension at the turn of the century with studies of succession. Clements (1916) noticed that orderly changes in plant associations led toward a more stable vegetative complex. The concept of succession leading to a stable climax in natural terrestrial communities had proven to be a durable paradigm for more than a quarter century (Clements and Shelford 1939).

Among zoologists a separate, more quantitative approach was being developed. Lotka and Volterra developed mathematical models which led to experimental work on equilibrium of two and three species interactions (Gauss 1934, Nicholson and Bailey 1935). This approach continues as an active field today (e.g., Rosenzweig 1971, May 1972a, Gilpin 1975, Tanner 1975, De Angelis, Goldstein, and O'Neill 1975).

Because of the separate conceptual developments by botanists and zoologists, one had to examine stability either in the light of plant communities or animal communities. Lindeman (1942) closed the gap with his holistic concept of trophic dynamics of ecological systems and set the stage for quantitative approaches to ecosystem stability.

There have been two major approaches to studying stability: static and dynamic. The static approach attempts to identify some property or indication of complexity (e.g., species diversity, connectivity, or energy balance) which may be measured at a single point in time and correlated with stability. The dynamic approach relies heavily on mathematical theory to examine the stability properties of models of the system. These approaches and their limitations will be considered in turn.

STATIC MEASURES AND CONCEPTS

Species Diversity

The notion of species diversity affecting ecological stability crept into the literature over a long period of time. For example, Elton (1958) notes numerous cases where simple communities are more easily upset than complex systems. In this context simple denotes less diverse. No one author can be clearly identified as the source of this concept. It is an underlying tone in much of the early literature.

Peet (1974) has identified a multitude of diversity indices, each index measuring slightly different information about species composition or abundance. Fisher (1943) first proposed species number (i.e., species richness) assuming all species could be found and taxonomically classified.

The Shannon Information Measure or Index was developed in 1949 (Shannon and Weaver 1949). Mathematically stated,

$$H_s = -\sum_{i=1}^{s} p_i \ln p_i \qquad (1)$$

where: H_s = the diversity in a group of s species

p_i = relative abundance of i^{th} species = $\frac{n_i}{N}$

n_i = number of individuals of i^{th} species

N = total number of all species.

This index considers relative abundance in addition to the number of species. The Shannon index can accommodate a large number of species, but can only be used to measure one class of biota at a time. It does not allow comparison of the relative importance of one compartment or trophic level with another.

Simpson's index (Simpson 1949) was the first to examine the heterogeneity of the sample:

$$\lambda = \sum_{i=1}^{S} p_i^2 \quad \text{(infinite sample index)} \qquad (2)$$

$$L = \sum_{i=1}^{S} [n_i(n_i-1)]/[N(N-1)] \quad \text{(finite sample index)} \qquad (3)$$

It is considered by many to be the weighted mean of the proportional abundance (Peet 1974).

Whittaker (1965) developed three related diversity measures: "alpha" diversity (within individual communities); "beta" diversity (along topographical gradients); and "gamma" diversity (resulting from both alpha and beta diversity).

In most diversity indices all age groups and species are assumed equal. Lloyd (1964) suggested weighting or correcting indices by sexual maturity. There are yet other measures of diversity (McIntosh 1967, Pielou 1966, Odum 1971) which have only increased the ambiguity and caused ecologists to question which index is best used in relation to ecological stability.

Trophic Level Connectivity

MacArthur (1955) proposed a stability index based on applying information theory and trophic transfer networks:

$$S = -\sum p_i \log p_i \qquad (4)$$

where p_i equals 1/N and N equals the number of choices of energy moving to the consumer, all links being equal.

Rutledge (1974) interpreted this index as the number of pathways that energy has to follow through the food web. If q indicates the

likelihood that a lower trophic compartment is an energy source of a higher trophic compartment, then p_{ij} is calculated by $p_{ij} = q_{ij} = q_{ji}$. Along with this index (4), MacArthur proposed the hypothetical maximum and minimum stabilities for each discrete number of species in a system. This approach became the focal point for a controversy of tundra versus tropic stability. Thus, MacArthur has been credited with developing the diversity-stability and connectivity-stability relationships.

It is interesting to note that after developing the stability index (4), MacArthur continued to use the Shannon information index, $H_s = -\Sigma p_i \ln p_i$ [note similarity to stability index (4)], as the sole diversity index in most of his work (MacArthur and MacArthur 1961, MacArthur, Recher, and Cody 1966, MacArthur 1967).

Geitopin (1972) discusses three approaches to trophic level connectance: (1) binary or set relations, (2) equivalence relations and (3) feeding relations. In binary and equivalence relations, animals are grouped by trophic level or assimilation efficiency into sets, and interactions are based on the Cartesian products of the set interaction. In feeding relationships, individual organisms or species are represented as points, and feeding interactions are shown by lines, trophic relationships by levels, and direction of energy transfer by arrows. He considers a food web as connected if every member is connected to at least one other member, and one must be able to reach every member of the food web through any other. Maximum connectedness (connectivity equals one) would have every member directly connected to every other member and the feeding relationship would be reciprocal. Anything less than maximum connectivity would have a value less than one. Connectedness and disconnectedness can be expressed:

Connectedness	Disconnectedness	
$\gamma = \frac{B}{\lambda}$	$\alpha = 1-\gamma$	(5)

where:

γ = connectedness

α = disconnectedness

λ = maximum possible connections $[(N-1)^2]$

B = actual number of connections

N-1 = number of members of food web -1, (assuming self feeding does not occur).

Gallopin (1972) discusses use of the elements of an N by N matrix, where each element indicates fractions of energy received by a population from each of the other populations.

Attempts have been made (de la Cruz and Wiegert 1967, Shure 1970, Shure 1973, Ratchie 1967, Wiegert and Odum 1969, McBrayer, Ratchie, and Auerbach 1970) to approximate trophic position or turnover rates in isolated food chains. However, the total or exact connectivity of a food web has never been measured exactly. Kercher and Shugart (1975) proposed a method which would determine connectivity by measuring standing crop biomass, but the general formulation to convert biomass to percentage connectivity has yet to be derived.

Canoy (1970) has made a unique attempt at measuring complexity of ecosystems based on milligrams of DNA m^{-2}. He found that mg DNA m^{-2} increased with progressive regularity of environmental conditions; however, failure to consider differences in species or abiotic portions of the system makes the results less useful.

Since the development of the first stability index there have been a number of attempts to generate other quantitative indices. Patten (1961) based his stability index on a matrix of transition probabilities. The stability measure is given by:

$$a = 1/N \sum_{j=1}^{N} \det P_j \qquad (6)$$

where:

a = stability of the system

N = number of variables

P_j = matrix of transition probabilities

$$P_j = \begin{bmatrix} P_{dd} & P_{di} \\ P_{id} & P_{ii} \end{bmatrix}$$

where P_{dd} represents the probability of a decrease in its value following an increase, P_{ii} the probability of an increase following an increase and so forth. Patten left this matrix unexplained and open to interpretation as to the methodology of calculation. This author has been unable to find any literature sources that have attempted to use this index in its initial form to measure stability.

Margalef (1969) developed his measure of ecological stability based on persistance of species over time. His stability index is given by:

$$S = (1/s) \sum_{i=1}^{i} b_i/m_i \text{ or } S = (1/s) \sum_{i=1}^{i} b_i t_i \qquad (7)$$

where b_i is equal to the fraction that any species (i) is of the total biomass of the ecosystem, m_i is the instantaneous mortality rate for that species, and t_i is the time necessary for the biomass of that species to be reduced to 50% of the original. Rutledge (1974) tied this measure closely to summing turnover times weighted by percent biomass of the

species. Again, as with Patten's (1961) index, little if any experimental work has been done using this index.

This literature generally assumes that greater diversity or food web connectivity implies greater ecosystem complexity. The question now remains whether these are truly system properties because neither measure considers abiotic components. More sophisticated measures, such as heterogeneity of physiological response or pattern diversity, are, again, only biotic measures. While these measures may be valid for their original applications to populations or to community analyses, their utility as measures of total ecosystem properties is questionable.

ENERGY BALANCE

Some ecology texts (Odum 1953, Odum 1959, Odum 1971) base stability on the second law of thermodynamics linked to succession and energy flow. H. T. Odum's (1957) work on energy dynamics of Silver Springs is a prime example of systems energetics approach. Using the definition of stability as constancy over time, it was demonstrated that mass energy balance is necessary to maintain community structure and composition. Lindeman (1942) and Ovington (1962) have also emphasized a balanced energy regime leading to stability. Although the energy balance approach appears to be dynamic, in actual practice, the single or seasonal measurement schemes often result in a static diagram which is then examined in search of insight into dynamic stability by implementing models.

The real dilemma arises from the fact that the second law states that the system should move towards increased randomness and hence increased disorder (Kormondy 1969), while observations of evolution

at both the organismal and the ecosystem level demonstrate just the opposite tendency (Clements 1916, Valentine 1968). Morowitz (1968) states that the second law of thermodynamics can only be applied to systems that are approaching equilibrium. For an ecosystem to fall into this select category for which the second law is applicable it would have to be either isolated or in contact with a single reservoir. Although approaching ecosystem stability through energy balance is an improvement over the diversity and connectivity approach, in that it deals with the total biotic portion of the system, the second law of thermodynamics is not applicable, because ecosystems are inherently open with energy sources and sinkes.

Studies and Controversies Based on These Indices

MacArthur's index (4) has caused much confusion and controversy. It was initially thought that MacArthur had concisely stated what had been an intuitive understanding for decades. He demonstrated that diversity was not the only critical criteria for stability, but that connectivity must also play an important role.

Elton (1958) focused on this concept in his discussion of arctic tundra versus tropical rain forest stability. Darlington (1969) indicates that species diversity increases by orders of magnitude as one moves from the polar regions to the equator. The concept that greater diversity implies greater stability had become conventional wisdom by the late 1960's. Bliss et al. (1973) raises further problems by arguing that arctic ecosystems are more fragile, not less stable, based on lower diversity and less available energy. Dunbar (1968) argues that through ecosystem evolution or succession, arctic ecosystems would acquire greater

diversity, eventually leading to greater stability. Yet, Amundsen (1975) holds that the maritime tundra of the Aleutian Islands does not undergo successional stages once disturbed. Dunbar (1973) suggests that tundra ecosystems are fragile and not unstable in the sense that they are capable of absorbing serious perturbations and eventually returning to equilibrium. Therefore, the controversy on stability, fragility, and succession in the tundra still exists with diversity shedding little, if any, light on the problem.

There have been a number of attempts to directly measure stability of natural and artifical ecosystems, based on MacArthur's (1955) stability index. Watt (1964) used four large data sets to determine whether numerical stability in insect populations was related to species diversity of food sources. Three of the four data bases had significant negative correlation and the fourth was not significant.

Paine (1966) examined three intertidal zones from Mukkan Bay, Washington, to the coast of Costa Rica. He based his study on subwebs of the ecosystem with a single top predator and with little transfer to other subwebs. When the top predator is artifically removed or naturally absent, the subweb evolved towards a less diverse and yet more stable unit. Thus, there is evidence that some trophic level control does exist, indicating diversity or connectivity is not the only stabilizing mechanism that should be considered.

Zaret and Paine (1973) examined tropical lakes into which a single species of predatory fish had been accidentally introduced. Comparisons with other lakes in the same region demonstrated a significant reduction in trophic web connectivity. The conclusion was reached that increasing

complexity (e.g.,diversity) did not necessarily denote increasing stability.

Hairston et al. (1968) conducted tests on a series of elaborate two- and three-trophic-level microcosms using bacteria, protozoa, and protozoan predators. Stability was measured by persistence of all species and by tendency to maintain equal distribution of numbers at each trophic level. Test results indicated that the diversity-stability concept did not hold in any of the experiments. There was important interaction of two protozoan species with the third species, indicating that interspecific competition may also play a role in stability.

Hurd et al. (1971) and Hurd and Wolf (1974) examined adjacent old fields of different ages, successional stages, and differing insect species diversities. The systems were simultaneously perturbed by nutrient enrichment. The systems were examined in relation to their ability to resist change in the arthropod community food web structure. It was concluded that stability of the food web was not related to higher diversity or successional age. Holt (172) commented that Hurd et al. (1971) had predetermined the results by selecting these particular age fields, location, and methods of sampling the arthropods.

Westwole and Levins (1972) examined the recolonization of mangrove islands before and after defaunation. Species were subsetted into trophic levels, and the time to return to original trophic level biomass structure and taxonomic composition was measured. The trophic level biomass distribution re-stabilized in 360-380 days; but, the taxonomic structure or diversity did not re-stabilize within that time frame. They concluded that trophic level dynamics were more important than species diversity.

While experimental tests were being conducted, theoreticians were still attempting to reenforce the hypothesis mathematically (Conrad 1972, Roberts 1974, Webber 1974). Leigh (1965) showed that absolute connectivity is possible by predator switching. Demetrius (1969), using Markov-chains, arrived at the same conclusions. Reddingius and den Boer (1970) introduced risk theory (i.e., spreading of dependence on any one food supply) to show reduced probability of system instability.

Rutledge, Bassore, and Mulholland (1976) developed an approach similar to MacArthur's index (4) (1955), utilizing a model that permits p_i to vary with time. They tested two ecosystems energy data bases and determined by simulation that both ecosystems reached maximum stability during the harshest environmental conditions.

There have been a number of attempts to approach stability from points other than diversity and connectivity. Golley (1974) examined twenty years of data on old fields for the ability to resist perturbations. He relates increasing stability to increasing community biomass. The greater the biomass the more resistant the community was to radiation exposure and the more rapidly it returned after plowing.

Ganf and Viner (1973) consider climatic fluctuations to be one of the key factors controlling shallow lake stability along with nutrient cycling. Boesch (1974) points out that low species diversity is influenced by low environmental constancy and that it is the environmental factors that influence stability. Pianka (1966), Cameron (1972), and Gates (1969) indicate that environmental constancy allows greater specialization (i.e., greater diversity) and this implies greater stability.

Dunbar (1973) expresses the opinion that arctic ecosystems, which are subject to environmental extremes, are more stable, even though they have low species diversity and cyclical population fluctuations, because they absorb perturbations more often.

A number of researchers have considered the influence of spatial heterogeneity on population constancy. Skellam (1951) applied random-walk theory to show that the greater the random dispersal of prey organisms the more constant the predator population will be. Huffaker (1958) concluded that spatial heterogeneity and physical barriers play a role in damping predator-prey oscillations. Spatial heterogeneity or pattern dispersal have surfaced continuously as a mechanism to explain stability since Huffaker's test of the hypothesis (Van Den Ende 1973, Roff 1974a, Roff 1974b, Comins and Blatt 1974, Wiegert 1975, Smith 1972).

Whatever static measurement has been adopted, significant problems have arisen in attempting experimental verification. This appears to be due to two factors. First, stability is a characteristic of the dynamic properties of the ecosystem. As such, it depends on both the structure and kinetics of the system. It is not surprising, therefore, that measures of structure alone have been unsuccessful. Second, as pointed out by Goodman (1975), the original diversity-stability hypothesis dealt with population and community stability and not with ecosystems. As a result, interaction with other biota, abiotic components, and factors such as spatial heterogeneity were largely ignored. These limitations have resulted in attempts to approach stability as a characteristic of the dynamic processes of a total ecosystem by quite different methods.

DYNAMIC STABILITY CONCEPTS

Lewontin (1969) criticized static approaches and emphasized that stability is a characteristic of the dynamic properties of an ecosystem. How do we know whether an ecosystem is stable, without knowing its response to a perturbation over time? Dynamic approaches to the problem have emphasized mathematical analysis of models of total systems rather than static measurements at a point in time.

Kerlin (1975) and May (1973c) have reviewed the techniques used in stability theory for dynamic systems. There are three normal approaches: (1) a system is stable if it is able to stay within a finite distance of the equilibrium condition after being subjected to a perturbation; (2) a perturbed system is stable if it returns to its original equilibrium point asymptotically; and (3) the system is considered unstable if it continually departs from its equilibrium conditions.

The dynamic stability approach seriously challenged conventional wisdom concerning the diversity-stability and connectivity-stability hypothesis (Gardner and Ashby 1970, May 1971, May 1973c). However, these approaches examine the dynamics properties of models and not ecosystems themselves under experimental conditions. This assumes that the models are valid and useful and truly reflect the stability of the ecosystem under question (Mankin et al. 1976). Therefore, danger exists in this technique without actual validation using real ecosystems.

Stability of Linear Models of Ecosystems

Linear unforced models are commonly described using matrix notation. A set of linear equations can be written as,

$$\frac{d\bar{x}}{dt} = A\bar{x} \qquad (8)$$

where A = (elements a_{ij}) is a matrix of constant transfer coefficients and $\bar{x}$ is a vector of state variables. The model is stable if it is negatively dominated on the diagonal, which implies that the eigenvalues (λ's, roots, or poles) have negative real parts (Funderlic and Heath 1971, Barnett and Storey 1970). This follows from the Gerschgorium Theorem, which states that the system is asymptotically stable if all P_i's are negative, where P_i is given by,

$$P_i = A_{ii} + \sum_{\substack{j=1 \\ i \neq j}}^{n} /A_{ij}/ \quad , \qquad (9)$$

A_{ii} is the diagonal element, and $\Sigma/A_{ij}/$ is the sum of the absolute values of the column elements (Kerlin 1975).

A forced linear constant coefficient model is defined by,

$$\frac{d\bar{x}}{dt} = A\bar{x} + f(t), \qquad (10)$$

where f(t) is the vector of forcing functions. The forced model is considered to be stable if the unforced system with the same transfer coefficients is stable (Kerlin 1975).

May (1971) examined multispecies community models and agreed with Gardner and Ashby (1970) that probability of model stability remained high as connectivity increases. However, at a critical percent connectance, the probability of stability rapidly decreases. Gardner and Ashby (1970) determined that the critical region was between 13 and 20%. Larger numbers of components in the system caused instability to occur more rapidly. The same conclusions were reached by Levins (1968) when examining increasingly complex biochemical processes of ecosystems.

A similar approach has been proposed by Levins (1974). Even when the exact transfer coefficients are not known, one can determine the model's stability through loop analysis, knowing only the sign of the matrix elements. There are two conditions necessary for stability using loop analysis: (1) At each level the negative feedbacks must outweigh the positive feedbacks, and (2) negative feedbacks with long-term lags must not be large relative to the short-term negative feedbacks. Jeffries (1974) discusses a similar approach using digraphs. Neither Levins' (1974) nor Jeffries' (1974) qualitative techniques have been tested experimentally.

There are also a number of graphical techniques used for evaluating model stability. Mikhailov's method or the modified Mikhailov method (Kerlin 1975) can indicate whether conditions are both necessary and sufficient for model stability but have not yet been applied to the analysis of ecosystem stability. Another graphical approach, the Nyquist method, has recently been introduced to predict the stability of a calcium cycle model (Shugart et al. 1976).

Various techniques exist to determine the relative stability of different systems. The Crucial Root method relies on the fact that the smallest eigenvalue (least negative) will control the time necessary for the system to return to a stable state. Other methods are Phase and Gain Margin techniques (Kerlin 1975). Waide et al. (1974) makes use of time domain and frequency response analysis when examining the calcium cycle in a forested watershed ecosystem. They relate stability analysis to ecosystem level properties, such as nutrient cycles, input-output budgets, and net ecosystem productivity.

May continues to point out that large complex ecosystem models are unstable as either percent connectivity or species number increases (May 1971, May 1972b, May 1973a, b, c, d). He notes that there are two major destabilizing features of the models: (1) time delay responses and (2) predator saturation. However, the model can be correspondingly balanced by two stabilizing factors; (1) density dependent fecundity and (2) predator switching. Lawton, Beddington, and Bonser (1974) observed and verified the switching phenomenon in certain insect predators as one of the stabilizing mechanisms.

There have been a number of papers branching off from May's work on linear and nonlinear ecosystem models. McMurtrie (1975) uses Monte Carlo techniques to generate random matrices and determined that a crude hierarchical scheme (i.e., organisms into trophic levels) imbedded in the model has a stabilizing effect. DeAngelis (1975) notes that if nonlinear food web models are characterized by low assimilation efficiencies, strong self-regulation in higher trophic levels, or a bias towards donor dependence, stability may increase with increasing connectance. Waide et al. (1974) maintain that the key to ecosystem stability is located in the system level properties and not in the diversity or connectance of food webs. Much of the early theoretical work used formal mathematical approaches under deterministic or constant environments. May (1973b) realized this fault and noted that if the stabilizing interactions among populations were strong, then a stochastic environment would have little if any effect on the stability of the system. However, the opposite was found if the interactions or associations were weak.

As one can see the problem has had extensive examination under linear systems analysis. Another approach has been taken for nonlinear stability analysis of models.

Stability of Nonlinear Models of Ecosystems

Kerlin (1975) points out that a number of phenomena appear in nonlinear systems which make them easily distinguishable from linear system, even when operating in the linear region of the model. A nonlinear system may possess both harmonics and subharmonics when excited by a sinusoidal input. A nonlinear system model may respond like a linear system to sinusoidal inputs up to certain frequencies where amplitude and phase may shift radically. Multiple equilibrium points and limit cycles are other characteristics exhibited by nonlinear models.

There are a number of phase plane diagrams which demonstrate nonlinear systems dynamics. Holling (1973) presents an excellent review of the use of these techniques for ecological systems. However, phase plane diagrams or isoclines are predominantly used in describing predator-prey interactions (Rosenzweig and MacArthur 1963).

The most important method of analysis is Liapunov's second or direct method (Liapunov 1907), which requires that an arbitrary function (V) be found, which is positive definite and contains all state variables. If $\dot{V}$ is negative definite the model of the system is asymptotically stable (Aggarwal 1972). Liapunov's direct method has had few applications in the analysis of nonlinear ecosystem models, but a number of recent articles have used it to test the stability of feeding populations in a community (Šiljak 1974, Šiljak 1975, Gilpin 1974, Ladde and Šiljak 1974, Shiao-Yen Wu 1974). The general conclusion is that nonlinear system

models become more stable as normal biological constraints are placed on the system or matrix. Samarjai and Goswami (1972) state that in nonlinear systems models the concept of critical connectance based on energy transfer in models may be meaningless or needs to be clarified.

There has been one unique approach to ecosystem stability using nonlinear Lagrange Theory (Thornton and Mulholland 1974). Lagrange stability is a topological approach which sets bounds on the transfer coefficients of the model and allows frequency oscillations to occur within those bounds. The limits set on the coefficients follow both mathematical and physical laws (i.e., laws of thermodynamics, laws of conservation of matter and energy). This method of nonlinear anaylsis has yet to be fully explored for applications to ecosystem stability.

The questions remain whether ecosystems are linear or nonlinear in their responses and which criteria should be used to realistically ascertain the stability of those ecosystems. Patten (1961) originally stated that linear stability analysis could not be applied because in general ecosystems are nonlinear. In a total reversal, Patten (1975), with some evidence but no conclusive proof, states that ecosystems in their climax stages are linear and that nonlinearity is selected against in the overall evolutionary self-design. May (1973c) presents this dilemma for open inspection by all ecologists. Shugart (1974) reviewed May's book and concluded that this should be the exit point for the diversity-stability roundhouse that has occurred over the last two decades.

Mechanisms for Dynamic Control of Ecosystem Stability

A number of mechanisms have been hypothesized as controls of ecological stability. As previously noted, DeAngelis (1975) indicates

that donor dependence, self-regulation of species and lower assimilation efficiencies increase food web model stability. Mattson and Addy (1975) state that forest production stability is controlled by phytophagous insects. O'Neill (1975) concludes that differences in turnover rates among system components can affect ecosystem stability. Dudzik et al. (1975) indicate that the organic detritus pool in the soil is the most important compartment to consider. They state that nutrient cycles or system's metabolism are the key factors, and not the system's cascading entropy that has been used as the stability indicator. Ecosystems stability is a characteristic of the dynamic processes and must be examined using dynamic system level parameters, which depend on all components of the system, not just aboveground biologically active food webs.

SYNOPSIS AND PROGNOSIS

Ecological stability has been approached from many perspectives in recent history. The concept has progressed from a level of intuitive understanding through diversity-stability and connectivity-stability at population and community levels and, more recently, to dynamic stability of system models. All approaches to stability have relied heavily on techniques of measuring system complexity and its relation to ecosystem stability.

In most cases the difficult, arises from the misinterpretation of the concept of ecosystems. Most ecologists consider only animal or plant populations, and generally only the aboveground portions. An ecosystem contains both biotic and abiotic components and is an externally forced, open system. Considering only the aboveground component ignores the fact

that in some forested ecosystems 80-90% of net forest primary productivity is cycled directly to the decomposers (Odum 1971). Most attempts have dealt with isolated portions of ecosystems and have not yet come to grips with either system complexity nor the ecosystem level concept. It is interesting to note that classical analyses were concerned with the aesthetics of the environment and we are still very close to this position today in our understanding of ecosystem stability.

Then where does the answer exist? Most ecosystem analysts agree that ecosystems have numerous properties or traits which should be measurable in a dynamic sense. The question then arises, what are those dynamic properties and how can they be measured? Once these questions have been answered, then ecosystem stability can be investigated forcefully. Some researchers have expressed doubts that such properties can be defined and measured. Levin (1974) states that, "it is clear that none [referring to systems properties] can be measured by a single variable." May (1974) states, "I have gloomy doubts as to the feasibility of providing any simple recipe whereby practical people may characterize the 'resilience' of an ecosystem."

From the questions initially posed in the introduction and from Levin's (1974) and May's (1974) remarks, the objectives and goals are set. These objectives and goals are to determine what ecosystem properties and traits are measurable, how those traits might be used to develop a new approach to ecosystem complexity, and how this measure of complexity relates to ecosystem stability.

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